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RATE OF MULTIPLICATION OF THE HESSIAN FLY.

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INTRODUCTORY AND HISTORICAL.

In the course of investigations of the Hessian fly (*Phytophaga destructor* Say) and its parasites, at the Cereal and Forage Insect Field Station of the Bureau of Entomology at Carlisle, Pa., it became necessary to have accurate data regarding the normal rate of multiplication of this insect. Such information was needed, in the first place, as a basis for estimating the efficiency of the various species of parasites. In the second place, the writer, having been greatly impressed by the rapidity with which an outbreak of serious proportions may develop in a short time from comparatively small sources, and being aware that such an increase is largely due to the reduction in effect of some of the important natural checks to the increase of the fly, suspected nevertheless that the potential rate of multiplication might be much greater than usually has been supposed.

The writer has been unable to find satisfactory data on this subject in the literature or among other recorded observations. In fact, it appears that little attention has ever been paid to the matter, especially

¹ Died June 23, 1920.

for males which are sure to emerge. Taking all of these facts into consideration, success beyond expectations was achieved in the fall of 1919, in making counts for the spring brood of 1920.⁶

AVERAGE NUMBER OF OVA FOR THE PRINCIPAL BROODS.

In presenting the results of this investigation, it will be necessary to consider first the average number of ova which can be laid by females of the principal generations. The data for each of these generations will be tabulated separately. After this has been done, it will be necessary to take into consideration the proportion of the two sexes before a sufficient basis can be had for estimating the rate of reproduction of the Hessian fly.

FALL GENERATION.

In Table 1 are given the results of counting the number of ova contained in 107 females. These flies were obtained from six different fields, as indicated by their cage numbers. It will be noted that the average number of eggs per female varies considerably in different fields, even when the number of females counted is approximately the same. It is thus easy to see what a difficult matter it is to obtain a fair average number of eggs per female. The figures, however, are as fair as could be obtained for the year in question and in the time available.

TABLE 1.—Average number of ova for females of the fall generation of the Hessian fly, Carlisle, Pa., 1919.

Cage No.—	Number of females counted.	Number of ova.	Minimum per female.	Maximum per female.	Range.	Average per female.
1620.....	28	8,014	74	383	309	286.0
1716.....	26	6,148	33	365	332	236.2
1753.....	36	13,422	189	464	275	372.8
1755.....	9	1,361	107	195	88	151.2
1779.....	6	1,099	134	302	168	183.2
1795.....	2	658	314	344	30	329.0
Totals.....	107	30,702	33	464	431	286.9

The actual number of ova per female varies from 33 to 464, with a range of variation of 431 and an average per female of 286.9. It may be added that the smallest female found since this work began belonged to this brood, but to none of the foregoing cage numbers. This female was dissected by Mr. Hill, who found that it contained only 11 ova. The largest female ever found belonged also to this brood. This female was in a different series and contained 474 ova.

⁶ In this connection the writer wishes to state that two lots of females of the fall brood were dissected by Mr. C. C. Hill; Mr. P. R. Myers has determined the sex of a large proportion of the flies as they emerged, and both men have helped in collecting and caging the material. All of the work has been done in the laboratory at Carlisle, Pa., and most of the material has been collected near by.

SPRING GENERATION.

For the spring generation the ova have been counted for 160 females. The most surprising thing about the results obtained, as shown in Table 2, is the general average number of ova per female of 232.9. This is an average of 54 eggs per female less than was found in the case of the fall brood.

TABLE 2.—Average number of ova for females of the spring generation of the Hessian fly; counts made at Carlisle, Pa., in the fall of 1919.

Cage No.—	Number of females counted.	Total number of ova.	Minimum per female.	Maximum per female.	Range.	Average per female.
1841.....	57	14,591	79	386	307	256.0
1842.....	29	6,990	113	372	259	241.0
1869.....	4	780	34	297	263	195.0
1875.....	13	3,105	188	350	162	238.8
1876.....	5	836	71	255	184	167.2
1880.....	8	1,356	102	214	112	169.5
1881.....	6	1,048	100	227	127	174.7
1882.....	2	483	194	289	95	241.5
1883.....	26	5,965	116	370	254	229.4
1891.....	10	2,106	108	309	201	210.6
Totals.....	160	37,260	34	386	352	232.9

While this work has been carried through only one spring generation, it is nevertheless quite evident that this generation is constantly lower than the fall generation in its capacity for egg production. The actual minimum number of ova per female is 34, which is one more than for the fall brood. The maximum, 386, on the contrary, is much lower, and the range of variation is only 352.

SUMMER GENERATION.

While data for the flies developing in volunteer wheat are scant, the results obtained seem interesting enough to be included as Table 3. Only 15 cases are available. In spite of the low average number of eggs, this brood in all probability resembles rather closely the fall generation in the number of eggs it can lay. If this should prove true, it might be that the stage of growth of the plant has an important relation to the size of the flies developing in a plant, and consequently to the number of ova developing.

TABLE 3.—Average number of ova for females of the generation of the Hessian fly developing in volunteer wheat; counts made at Carlisle, Pa., in the summer of 1919.

Cage No.	Number of females counted.	Total number of ova.	Minimum per female.	Maximum per female.	Range.	Average per female.
1990.....	2	524	177	347	170	262.0
2090.....	13	3,027	54	448	394	232.8
Totals.....	15	3,551	54	448	394	236.7

SEX RATIO.

Before proceeding further with the discussion of the rate of multiplication, it is necessary to take up the question of the proportion existing between the two sexes. In order to acquire data on this subject, a beginning was made, more than two years ago, to record the sex of all Hessian flies that emerged in the cages. These cages contained only puparia separated from their surrounding plant tissue and reared in small vials. The puparia had been obtained in various localities in the northeastern portion of the United States. In this way the sex has been recorded of practically every fly that has emerged from a few thousand puparia each year. At the end of the first year it appeared that the percentage of females in the spring generation was remarkably high. It was not anticipated that this excess of females in the spring generation would prove to be constant, but Table 4 shows that for the second year the percentage of females dropped only slightly. Although the rearing of flies from the 1919 material has not been completed, a much larger number than usual have already been obtained, and the percentage of females for 1919 is almost the same as for the two preceding years.

TABLE 4.—*The sex ratio in the various Hessian fly generations, 1917, 1918, and 1919.*

Generation.	Year.	Number of males.	Number of females.	Total reared.	Per cent of females.
Spring.....	1917	168	276	444	62.2
	1918	146	235	381	61.7
	1919	623	1,031	1,654	62.3
Fall.....	1917	749	761	1,510	50.4
	1918	1,493	1,313	2,806	46.8
Volunteer wheat.....	1917	246	225	471	47.8
	1918	51	45	96	46.9

For the three years the average percentage of females is 62.1, and it seems quite safe to assume now that at least 60 per cent of the spring brood develop into females. In the case of the fall generation the sexes appear to be approximately equal in numbers, although figures for 1918 are rather low in females. In volunteer wheat there are a very small number of cases from 1918, but it appears in general that the sexes are about equal in the partial broods developed in the summer.

It is now evident enough that the spring brood is the one which shows the greatest variation from normal, both in the high percentage of females produced and in the reduced number of eggs these females can lay. Both may be related phenomena with a common explanation, but this explanation will have to be left to the imagination at the present time.

THE MEANING OF THESE FIGURES.

In order to demonstrate fully the meaning of the figures which have been submitted, two examples will be of considerable help.

Going on the assumption that under normal conditions practically every egg is laid, let it be assumed that none of the fly stages are destroyed by enemies. For the sake of round numbers let 285 be taken as the average number of eggs laid by the fall generation and 230 as the average by the spring generation. It may also be taken for granted that one male will fertilize several females, since Enock⁷ proved by careful methods that one male successfully fertilized as many as six females. This will take care of the preponderance of females in the spring brood.

Starting now with a single female of the spring brood emerging in the fall, it is found that she can lay 230 eggs. One-half of these eggs in the spring will produce females, each of which may lay 285 eggs. This will give 32,775 as the product of one female working through two generations in one wheat crop, with no allowance made for multiplication in volunteer wheat. The flies which develop in volunteer wheat in the East are usually comparatively small in number and are heavily parasitized. If it be assumed that all these flies remain alive in the stubbles until the next fall, there will be a total of 60 per cent of the flies emerging as females, or 19,665. If these all lay 230 eggs, there will be the enormous total of 4,522,950 flies developing in the fall wheat of the second year. The resulting females would number 2,261,475 and would give rise in the second spring to 644,520,375 fly stages. This result has been obtained in two crop years, not allowing for any multiplication in volunteer wheat.

The question may be looked at from another point of view. Probably infestation of stubbles is never as low as one puparium per acre, although the foregoing computation began with one fly. In one field studied quite carefully during the summer and fall of 1919 the stubbles were found to be infested at the rate of 4,900,000 per acre. A careful examination of the puparia in these stubbles just before the emergence season showed that only 4.4 per cent contained living fly larvae, parasites having destroyed practically all of the remainder. This 4.4 per cent amounts to 215,600 flies per acre. If 60 per cent of these were females there would be 129,360 females per acre ovipositing in the next crop of wheat and producing in it the next fall 29,752,800 ova. With similar calculations from a few other fields as a basis, a big outbreak in wheat sown in the fall of 1919 was looked for. As a matter of fact, however, it was found after the emergence season was over that many of the expected flies had failed to emerge from the stubbles. A careful count made in the field mentioned above showed that only about one-third of the healthy fly larvæ had transformed. This amounted to about 1.4 per cent of the total number of flies.

⁷ Op. cit.

Correcting the figures to correspond with what actually happened in the field and calculating in the same way as before, it is found that this extremely small percentage of flies transforming in this stubble field in the fall would amount to 68,600 flies per acre, with 60 per cent or 41,160 females. These females would lay enough eggs to develop into 9,466,800 flies per acre in young wheat sown in the fall of 1919. This is a much smaller number than had been anticipated, but it will be readily seen that even this is an enormous infestation. If the farmer sows about the same acreage from year to year and no flies are lost by migration, then the flies from an acre of stubbles would proceed to an acre of new wheat. It is calculated that 1,000,000 plants per acre is a good stand, and in that case this farmer would have over nine flies developing on every wheat plant. It will be readily seen from this that his chances of securing a wheat crop under the conditions named are practically zero. It is also evident that anything which helps to cut down this rate of reproduction is of enormous benefit. The principal checks to the multiplication of the Hessian fly are its parasitic enemies and unfavorable weather conditions, and if it were not for them it probably would be impossible inside of two years to grow wheat at all. This illustration, it is hoped, will also help to explain how an outbreak may seem to develop suddenly from a very low infestation of stubbles.

CONCLUSIONS.

The principal points made in this bulletin may be summarized as follows:

1. The rate of multiplication of the Hessian fly is much higher than has been realized.
2. The rate of multiplication is quite different in the two principal broods of the Hessian fly, the spring brood laying on an average only about 230 eggs per female, whereas the fall brood lays about 285 eggs per female.
3. The capacity for reproduction also varies with a number of other factors, such as date of sowing, number of puparia per tiller, etc.
4. Because of these various influences, the actual rate of multiplication will be found to vary from year to year and even from field to field, and in years of light infestation the figures will prove too low.
5. The proportion of males to females varies in the two principal generations. In the spring generation about 60 per cent of the flies are females; in the fall generation the sexes are approximately equal in number.
6. By applying these figures, however unsatisfactory the basis may be, it is believed that entomologists will be better able to appreciate how a Hessian fly outbreak may develop very suddenly, and to predict in a more accurate manner the approach of a dangerous outbreak.